

THE TRIASSIC FISH *SAURICHTHYS* *KRAMBERGERI* SCHLOSSER

by JOHN GRIFFITH

ABSTRACT. This paper gives a detailed account of the unique holotype of *Saurichthys krambergeri*. A figure of this specimen was published as long ago as 1918 but, apart from a brief reference to it by Stensiö, it has not previously been described. The illustrations include an attempted reconstruction of the skull. The structure of the teeth shows that some of Stensiö's views concerning the teeth of saurichthyids are no longer tenable, and it is concluded that there are no characters which enable species to be referred to the genus *Saurichthys* solely on the basis of tooth structure. The relationship of the angular and dentary bones is compared with the condition in other species of *Saurichthys* and in the genus *Saurorhynchus*. The reduction in the squamation and the large size are discussed.

Saurichthys krambergeri has been known for more than forty years, but no comprehensive description has been published. The earliest reference to this species occurs in the third edition of Zittel's *Grundzüge der Paläontologie (Paläozoologie)*, *Abt. 2* (1918). In the section on fishes, revised in this edition by M. Schlosser, there appears a drawing of an almost entire saurichthyid fish with the legend '*Saurichthys Krambergeri*, Schlosser. Obere Trias. Adnet bei Salzburg'. There is no mention of this species in the text. In the fourth edition of Zittel's text-book (Zittel 1923) the same illustration is reproduced but to the legend has been added '1/8th nat. gr.'; again there is no mention in the text. Stensiö (1925) refers to certain features of the anatomy of *S. krambergeri*—notably the structure of the vertebral column—but does not give a full description or include any illustrations of this species.

I wish to express my gratitude to Professor Dr. Richard Dehm, Director of the Bayerische Staatssammlung für Paläontologie und historische Geologie at Munich, for permitting me to examine the holotype of *Saurichthys krambergeri* and other valuable specimens in his care, and for providing me with facilities for doing so. I am also grateful to Dr. K. Werner Barthel for his invaluable assistance and to the technical staff of the museum for the preparation of photographs and casts.

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SYSTEMATIC DESCRIPTION

Saurichthys Krambergeri M. Schlosser 1918, fig. 158.

Saurichthys krambergeri Schlosser. E. A. Stensiö 1925, pp. 180–1.

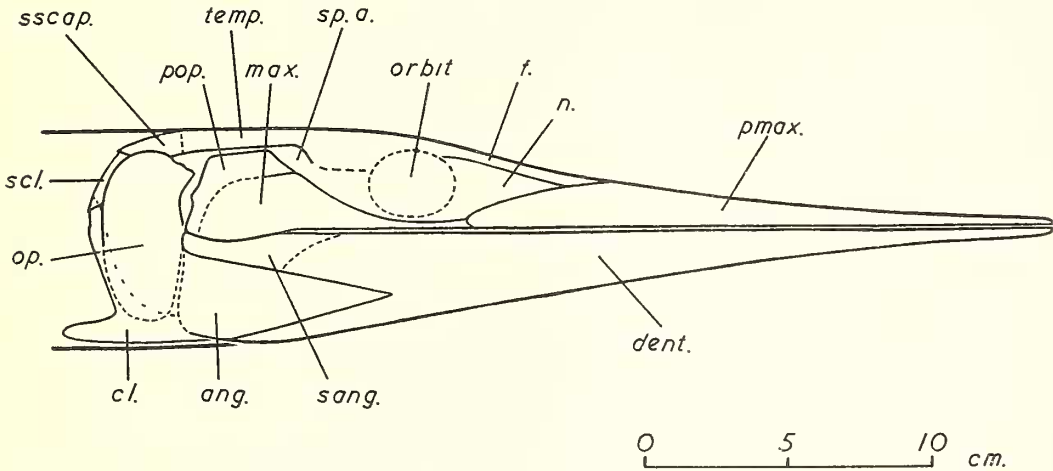
Belonorhynchus krambergeri (Schlosser). A. S. Woodward 1932, fig. 191.

As Reis (1892) and Stensiö (1919, 1925) have shown, the generic name *Belonorhynchus* Bronn 1858 is a synonym of *Saurichthys* Agassiz 1834. The specific name *Saurichthys krambergeri* therefore has priority over *Belonorhynchus krambergeri*.

Diagnosis. Large teeth of the dentition with the following characteristics: apical cap occupying approximately half of the tooth height; basal portion of tooth with moderately prominent ridges; apical cap bearing well-marked, coarse ridges but no keels; pulp

cavity extending nearly to tooth apex. Dentary relatively large and extending posteriorly ventral to the angular. Scales restricted to two longitudinal rows. Fin ray numbers: pectoral 32; pelvic 25; dorsal 38; anal 27+; caudal-epicaudal lobe 32, hypocaudal lobe *c.* 32. Rays of pelvic fin unjointed, otherwise all fins contain some rays which are both jointed and branched. No fulcral scales present.

Holotype. The almost complete skeleton of a large fish preserved lying on its side. The specimen, which comes from deposits of Upper Triassic age at Adnet, near Salzburg in Austria, is in the Bayerische Staatssammlung für Paläontologie at Munich (specimen number 1910/1/8). No other material of this species has been recorded.



TEXT-FIG. 1. *Saurichthys krambergeri*. Reconstruction of skull in lateral view. ang., angular; cl., cleithrum; dent., dentary; f., frontal; max., maxilla; n., nasal; op., opercular; pmax., premaxilla; pop., preopercular; sang., supra-angular; scl., supracleithrum; sp.a., position of spiracular opening; sscap., suprascapular; temp., temporal.

Measurements and proportions

Total length 113.0 cm.

Maximum depth of trunk *c.* 7.0 cm.

Length of skull (including operculum) 32.8 cm.

The body is very long and slender and the head occupies a considerable proportion (29 per cent.) of the total length (Plate 50, fig. 1). The pectoral fins lie close behind the operculum. The small pelvic fins are placed a little nearer to the operculum than to the caudal fin. Posterior to the dorsal and anal fins the body tapers to the slender caudal peduncle which bears the large, bilobed caudal fin.

The skull. The head is prolonged into a long, sharply pointed beak, in the formation of which both upper and lower jaws are involved (Plate 50, fig. 2). Owing to the method of preservation comparatively little can be made out of the bones of the skull roof. Most of the larger elements forming the side of the head can be distinguished, and these are shown restored in text-fig. 1.

The orbit appears to have been of moderate size, though its entire boundary could not

accurately be determined; a small portion of the sclerotic ring can be seen just in front of its posterior margin.

The premaxilla is an elongated element which, in addition to occupying approximately two-thirds of the edge of the upper jaw, also covers nearly all of the lateral and dorso-lateral surface of the rostrum. The two premaxillae appear to be in contact dorsally, at and near their anterior ends. Farther back they may have been separated by one or more postrostral bones or they may have remained in contact with each other as far as the anterior limits of the frontals, but it is impossible to decide this from the specimen. Posteriorly the premaxillae end level with the anterior limit of the orbit. The maxilla has an expanded posterior portion which forms a considerable part of the side of the skull posterior to the orbit, and a slender anterior part which extends forwards beneath the orbit to meet the premaxilla. The posterior portion of the maxilla is in close contact along much of its dorsal and its entire posterior margin with the preopercular. Part of the suture between these two bones can be distinguished in the specimen; the remainder probably followed the path indicated by the broken line in the reconstruction. In the posterior part of the maxilla the ventral edge projects downwards in a gentle curve and overlies the dorsal edge of the mandible. The preopercular can also be considered to consist of two parts: an expanded dorsal portion which lies dorsal to the maxilla, and a narrower ventral part which lies posterior to the maxilla. The nasal is a roughly triangular bone lying with its apex directed forwards. Its concave posterior margin seems to have formed the anterior limit of the orbit. The exact shape and extent of the frontals cannot be determined. They were probably in contact with each other in the mid-dorsal line, and they appear to have formed part of the dorsal margin of the orbit. Anterior to the orbit the frontals extend forwards above and between the nasals to make contact with the premaxillae. Part of the lateral edge of the temporal bone can be seen. This runs near to, and parallel with, the dorsal edge of the preopercular but the two bones were not apparently in direct contact. The lateral margin of the temporal continues forwards in a straight line but turns ventrally a little distance in front of the anterior limit of the preopercular so that these two bones partly enclose a gap in the dermal bony covering of the head. Stensiö interprets a similar space in the skull of *Saurichthys ornatus* as marking the position in life of the external opening of the spiracle (Stensiö 1925).

The mandible is very powerfully built. Posteriorly it is as deep as the remainder of the skull is high. Anteriorly it appears to end a little distance behind the extreme anterior end of the upper jaw. Careful examination, however, shows that the tip of the mandible is missing in the specimen so that it was originally somewhat longer and in the reconstruction I have shown it as equal in length to the upper jaw. The posterior margin of the exposed right mandibular ramus is damaged and is tentatively restored in the figure. The dentary is remarkable both for its large size and for the development of a process which extends posteriorly for a considerable distance ventral to the angular. Due to the presence of this prolongation of the dentary the angular too is unusual when compared to other saurichthyids in regard to its shape, which is roughly that of an isosceles triangle

EXPLANATION OF PLATE 50

Fig. 1. *Saurichthys krambergeri*. Holotype. Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich. 1910/1/8.

Fig. 2. *S. krambergeri*. Skull of holotype.



GRIFFITH, *Saurichthys krambergeri*

with the apex directed forwards, and also in the very small extent to which it contributes to the ventral margin of the mandible. A considerable part of the antero-dorsal edge and more than three-quarters of the antero-ventral edge of the angular are in contact with the dentary. The remainder of the antero-dorsal edge is in contact with the supra-angular element and the posterior edge of the angular forms nearly all of the posterior margin of the mandible. The supra-angular is poorly preserved. Nevertheless a good idea of its shape can be obtained as the fragments present include the posterior edge and part of the dorsal edge of the bone, and further information is given by the well-marked antero-dorsal margin of the angular. The exact position of the suture between the supra-angular and the dentary could not be determined; its approximate position is indicated in the reconstruction by a broken line.

The opercular region can be interpreted in one of two ways depending upon whether or not a separate subopercular bone was present originally. The remains represent either an almost entire right opercular, seen partly in impression and with its ventral edge missing, and ventral to this the major part of a less well-preserved left subopercular, or, alternatively, rather more than the dorsal half of the right opercular and the ventral portion of the left opercular. In all saurichthyids in which the opercular region is known the operculum was supported solely by the large opercular bone and no subopercular bone is present. In the absence of evidence to the contrary it should therefore be supposed that this was also the condition in *S. krambergeri* and so the second of the two alternative interpretations given above must be adopted. In this case the operculum appears to have been approximately twice as high as it is long. Antero-dorsally it is produced into an angle but apart from this is roughly oval in shape. No branchiostegal rays can be distinguished.

Nothing can be seen of the sensory canal system.

Over much of the skull the external surface of the dermal bones has been damaged or is poorly preserved, but elsewhere it is possible to see something of the superficial ridges and pits with which these bones were ornamented. The lateral surfaces of the premaxilla and dentary, and much of the surface of the maxilla and preopercula, bear numerous, very fine, parallel ridges. These run, for the most part, approximately at right angles to the edge of the jaw, but those on the dentary tend to be inclined slightly more towards a postero-dorsal—antero-ventral direction. In certain areas these fine ridges are replaced by rather coarser ones. On the dentary, these coarse ridges lie near the ventral edge of the bone. In the anterior three-quarters of this bone, they run roughly parallel to the ventral edge; in the posterior quarter, they are irregular in their disposition. On the angular, they appear to radiate from the postero-ventral angle of the bone. On the preopercula, they radiate from the postero-dorsal angle of the bone, but are somewhat irregular and tend to anastomose so as to enclose shallow depressions or pits. Beneath the orbit, the maxilla bears coarse ridges which run parallel with the edge of the jaw, but a little farther back the ornament takes the form of anastomosing ridges. The antero-dorsal part of the opercular bone is pitted. The remainder of the bone shows faint concentric growth-lines and very fine, parallel ridges running mainly in a dorso-ventral direction but curving forwards a little near the upper margin of the bone.

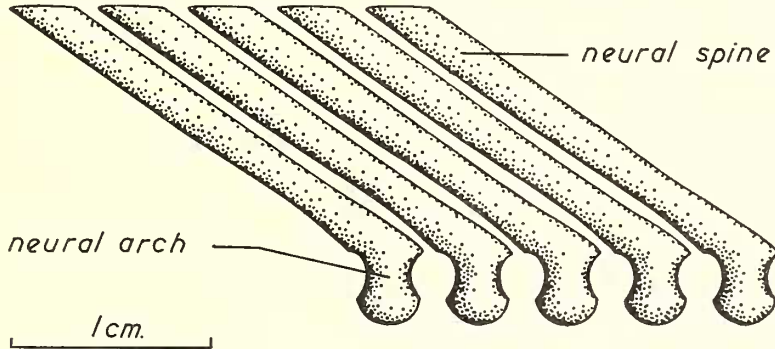
The most conspicuous feature of the dentition is the presence, in approximately the anterior third of both upper and lower jaws, of a series of large conical teeth. In the specimen some of the large teeth have been broken away; the number originally present in

both the right upper jaw and the right lower jaw appears to have been thirteen. These teeth are arranged so that those of the upper jaw fitted between those of the lower jaw in occlusion. Opposite some, at least, of the large teeth the bone of the opposing jaw contains depressions into which the tooth apices fitted. The teeth are bluntly conical in shape, and are very gently curved so that their apices are directed slightly backwards. They show no sign of lateral compression, i.e. they are approximately circular in section. Each tooth is clearly differentiated into an apical cap composed of vitrodentine and a basal portion of orthodentine. Several of the large teeth are badly worn, some showing well-marked wear facets caused by repeated contact with teeth of the opposing jaw. Measurements were taken from eight of the least damaged of the large teeth. The height of these teeth ranges from 3.3 mm. to 5.2 mm. On average, the tooth height is approximately twice the diameter of the tooth base, and the apical cap occupies a little more than one-half (55 per cent.) of the total height. The basal portion of each tooth bears moderately prominent ridges. These run in a general basal-apical direction but are slightly irregular and tend to anastomose. The apical cap is roughly conical in shape. Its height is, on average, one and a half times its maximum diameter. The surface of the apical cap bears a number of coarse ridges which run from the base of the cap towards the tooth apex but there is no indication of the development of the prominent keels such as are found in *Saurichthys apicalis*. In some of the teeth the vitrodentine of the apical cap is sufficiently transparent to allow the pulp cavity to be seen without any further preparation. It is interesting to notice that in these teeth the pulp cavity extends for a considerable distance into the portion of the tooth covered by the apical cap, reaching nearly to the tooth apex.

Between the large teeth which have just been described lie more numerous smaller teeth, the largest of which attain a height of approximately 2 mm. These smaller teeth appear to be of similar appearance to the large teeth but are less well displayed in the specimen.

Vertebral column. In the specimen the vertebral column is represented by a continuous series of ossified dorsal elements, and a number of ossified ventral elements lying in the region of the caudal fin; there is no trace of vertebral centra. It seems probable that in life a persistent notochord was present and also that the row of ventral elements was completed by cartilaginous structures lying anterior to the ossified ventral elements present in the caudal region of the fossil. Each dorsal element is composed of a neural arch to which is attached a long neural spine (text-fig. 2). Each neural arch consists of a pair of curved bony plates which extended one on either side of the spinal cord and probably made contact with the dorso-lateral surfaces of the notochord. The ventral margins of the neural arch are convex. Both the anterior and the posterior margins are markedly concave, and the concavities of contiguous neural arches are so arranged as to form a series of relatively large oval spaces between them, which must have served for the emergence of the spinal nerves. Successive neural arches though close together are not directly in contact and bear no articulating processes. The neural spines are stout and slope backwards at an angle of approximately 35° to the long axis of the vertebral column. In species of the family Saurichthyidae where the structure of the vertebral column is known in some detail, e.g. *Saurichthys madagascariensis* (Lehman 1952) and *Saurorhynchus brevirostris* (Hauff 1938), the neural spines have been shown to be double

structures composed of separate left and right ossifications which were probably joined in life by cartilage or fibrous tissue. It is impossible, owing to the manner in which the vertebral structures are preserved, to determine the exact condition in *Saurichthys krambergi*. However, the fact that in the specimen none of the neural spines appears with left and right halves displaced relative to one another seems to indicate either that the neural arches are single, i.e. median structures, or alternatively if they are double structures that the left and right halves were firmly joined together. In the trunk region



TEXT-FIG. 2. *Saurichthys krambergi*. Reconstruction of ossified dorsal vertebral elements of the trunk region in lateral view. Anterior to the right.

each neural arch is approximately 4 mm. in height, and each neural spine approximately 20 mm. long. The arrangement of the vertebral elements in the caudal pedicel is concealed by the enlarged scales present. Within the caudal fin the neural spines supported the fin rays of the epicaudal lobe. The termination of the vertebral column is not preserved. Ossified haemal arches and haemal spines are present in the region of the caudal fin where they served to support the hypocaudal lobe.

The total number of vertebrae present appears to have been approximately 190.

Appendicular skeleton. Nothing can be seen of the endoskeletal part of the pectoral girdle. The dermal bones, however, are visible and these consist of the suprascapula, supracleithrum, and cleithrum; there is no clavicle. The suprascapula and supracleithrum are both small, slightly curved bones. The anterior end of the former was in contact with the temporal bone of the skull roof. The cleithrum is a large bone composed of a relatively broad ventral portion lying parallel to the long axis of the head, and a more slender dorsal process lying approximately at right angles to it. The ventral portion tapers slightly towards its rounded posterior end; anteriorly it extends forwards mesial to the mandible but its full extent in this direction cannot be ascertained. Approximately the lower half of the dorsal process of the cleithrum bears moderately fine, irregular ridges on its external surface. Surface detail is not preserved on the remainder of the pectoral girdle.

The right pectoral fin is well preserved. It is roughly fan-shaped, of moderate size, and contains approximately thirty-two fin-rays. The anterior rays increase in thickness and in length until the fifth or sixth ray, after which there is little change in the length of the fin-rays though they become gradually more slender. The most anterior rays are slightly curved, unbranched, and show no sign of transverse joints. From about the sixth ray

backwards the fin-rays become less curved and branch distally. The more anterior to these branching fin-rays are unjointed and fork once only. The more posterior rays branch into four and appear to have been jointed for a little distance proximal to the level at which they branch.

The pelvic girdle is not preserved. The pelvic fins are slightly smaller than the pectoral and are roughly triangular in shape with a curved anterior margin. Both fins are present in the specimen but the right fin is better preserved than the left. It contains at least twenty-five slightly curved rays none of which appears to have been jointed. The anterior rays increase rapidly in length until about the fifth ray which is the longest in the fin and also the stoutest. After this the fin-rays become gradually shorter and more slender. The most anterior rays, up to and including the longest ray, are unbranched, the remainder fork distally; some at least into four.

Both dorsal and anal fins were supported by a number of ossified, radial elements lying within the body and at an angle of approximately 25° to the long axis of the vertebral column. These structures are poorly preserved in the specimen, but are considerably less numerous than the fin-rays which they supported, and appear to have corresponded in number to the vertebrae in this region.

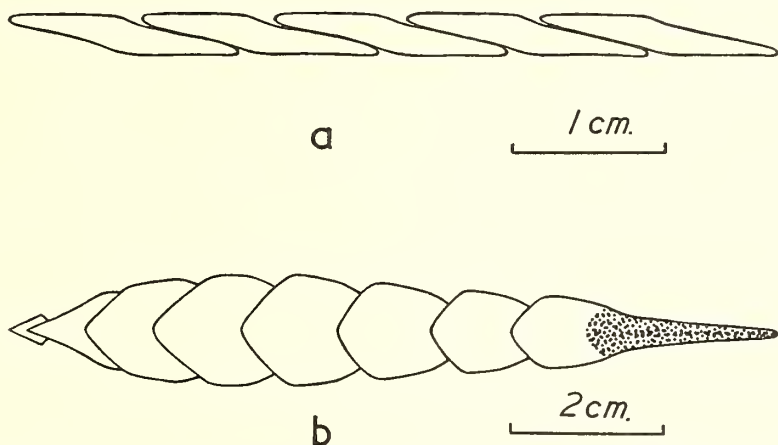
The dorsal fin is large, having a maximum height of 9 cm. and a length of 8 cm. It is roughly triangular in shape with a curved anterior margin and contains approximately thirty-eight rays all of which are jointed. The longest and stoutest ray is probably the eleventh or twelfth from the commencement of the fin, though owing to the small size and poor preservation of some of the most anterior rays it is impossible to determine with accuracy the number of rays preceding it. This ray and the rays anterior to it are unbranched; the remainder branch distally into four. The rays in the anterior part of the fin are noticeably stouter than the more posterior rays.

The anal fin is placed a little farther from the head than is the dorsal, the most anterior ray of the former being opposite to the seventh ray of the latter. It is less well preserved than the dorsal but appears to have been originally of approximately the same size and shape. The anal fin contained at least twenty-seven rays all of which are jointed. The longest and stoutest ray is the tenth or eleventh. The anterior rays are unbranched, the remainder branch distally into four. As in the dorsal fin, the rays in the posterior part of the fin are more slender than those in the anterior part.

The caudal fin is large and bilobed. Internally the epicaudal lobe was supported by ossified neural spines and the hypocaudal lobe by ossified haemal spines. The portion of the vertebral column contained within the caudal fin appears to have been straight and in line with the long axis of the body. In both lobes the fin-rays are more numerous than the endoskeletal supports. The epicaudal lobe measures approximately 8 cm. in height and contains approximately thirty-two rays all of which are repeatedly jointed. The longest ray is probably the twelfth. This ray and the rays anterior to it are unbranched and relatively stout. The rays posterior to the longest ray decrease in relative thickness as well as in length, and branch distally, some, at least, into four. The hypocaudal lobe is partly damaged but the portion preserved closely resembles the corresponding part of the epicaudal lobe.

Squamation. The scales are limited to two longitudinal rows, one in the mid-dorsal line and the other in the mid-ventral line. The lateral line scale rows found in the majority

of saurichthyids appear to have been absent in this species. The scales of the mid-dorsal row commence immediately behind the skull. As far as the level of the pelvic fin they are stoutly needle-shaped and approximately 14 mm. long (text-fig. 3*a*). Behind this region they increase gradually in size until the dorsal fin which interrupts the scale row. The scale immediately in front of the dorsal fin has a length of 28 mm. and is relatively broader than the more anterior scales. Posterior to the dorsal fin—on the caudal peduncle—the



TEXT-FIG. 3. *Saurichthys krambergeri*. Reconstructions of: *a*, part of dorsal scale row in mid-trunk region in lateral view; *b*, part of ventral scale row immediately anterior to caudal fin in ventral view. The stippled area in *b* indicates the part of a scale which was originally covered by the preceding scale. In both *a* and *b* anterior is to the right.

scales of the mid-dorsal row are not so well preserved as those of the mid-ventral row and only their internal surfaces are exposed. It is obvious, however, that they are similar to the corresponding scales of the mid-ventral series (described below) and also that they are well developed and considerably broader than the scales anterior to the dorsal fin.

There are no scales of the mid-ventral series preserved in the anterior trunk region. This may be either an accident of preservation or else the scale row may have started some distance behind the head. In the region of the pelvic fins the mid-ventral scale row appears to have divided into two and then reunited so as to form an oval, anal loop, though the exact arrangement of the scales could not be determined. With the exception of the features described above the scales of the mid-ventral series appear to have been exactly like the corresponding scales of the mid-dorsal row. On the caudal peduncle the ventral scales are better preserved than the dorsal scales and so will be described in greater detail. Roughly ten scales lie in this region (text-fig. 3*b*). The first eight scales after the anal fin are very well developed and each has an overall length of approximately 35 mm. The exposed posterior parts of these scales are broad and shield-shaped with the apex of the shield directed posteriorly and fitting into a V-shaped notch in the anterior edge of the exposed part of the succeeding scale. In the two broadest scales—the sixth and seventh from the anal fin—the exposed portion measures 14.5 mm. in width and has a length in the mid-ventral line of 12 mm. The external surface of each of these eight scales bears rather irregular, anastomosing ridges which show a slight tendency to radiate from the centre of the exposed portion. The internal surface of the exposed part

is smooth but bears a prominent median keel. The unexposed part of the scale, which was embedded in the dermis, is narrower than the exposed portion and is unornamented. Its inner surface bears a keel continuous with that found on the inner surface of the exposed part of the scale. Its outer surface shows a well-marked longitudinal groove for the reception of the keel on the inner surface of the preceding scale. The two scales immediately in front of the hypocaudal lobe of the caudal fin are less well developed than the other scales on the caudal peduncle. Their exposed portions are unornamented, narrower and more triangular in outline, but these scales are still considerably broader than any anterior to the anal fin.

Except for those regions of the body where the scale rows are interrupted, the scales of each row are exactly half as numerous as the neural arches.

DISCUSSION

In many features of its skeleton, *Saurichthys krambergeri* resembles other species of the Saurichthyidae and so may be considered to be a fairly typical member of the family. There are, however, several features worthy of comment.

The Structure of the Teeth. The large teeth of *S. krambergeri* differ from those of the other species of the genus in which the tooth structure is known, both by the possession of coarse ridges on the apical cap and by the extent of the penetration of the pulp cavity into this portion of the tooth. In the past, several authors have assumed that the teeth of members of the genus *Saurichthys* share a number of distinctive features which enable isolated teeth to be identified as having been originally part of the dentition of a fish of this genus, but, with the exception of Stensiö, they have failed to indicate clearly what these special features are. In 1925 Stensiö enumerated the following distinctive characters—mainly as a result of his work on the Spitsbergen saurichthyids. He considered the teeth of *Saurichthys*, in so far as they were then known, to differ from those of *Birgeria* by the following characters:

- (1) the pulp cavity does not extend—or extends only very slightly—into the distal part covered by the enamel cap;
- (2) the orthodentine in and close to the base is developed as simple plici-dentine;
- (3) the enamel cap is either smooth or with an extremely fine vertical wrinkling, but never with coarse, sharp, raised striae.

However, if one considers the teeth of *S. krambergeri*, which in all other respects appears to be a typical saurichthyid, it becomes clear that none of Stensiö's criteria can stand. For in these species: (1) the pulp cavity extends as far into the apical cap as in *B. acuminatus* or *B. mougeoti*; (2) the basal portion of the tooth shows no sign of the development of even simple 'plici-dentine'; (3) the apical cap bears striae which are as well developed as those of *B. acuminatus*, *B. mougeoti*, or *B. stensiöi*. An examination of a number of species of *Saurichthys* shows that in fact, apart from the simple conical shape and the division of the tooth into a basal portion composed of orthodentine and an apical cap of vitrodentine, neither of which is an exclusive feature, the teeth of the genus *Saurichthys* show considerable interspecific variation. This makes it doubtful whether this genus possesses any tooth characters, or combination of tooth characters, which are diagnostic. It follows from this that the referring of species, based on fragmentary remains, to the genus *Saurichthys* on the basis of tooth characters alone cannot be justified, and that such identifications must be regarded with suspicion.